BULLETIN

OF THE

BROOKLYN ENTOMOLOGICAL SOCIETY

VOL. XXXI OCTOBER, 1936 NO. 4

SUGGESTIONS FOR A NEW INTERPRETATION OF THE POSTABDOMEN IN MALE CYCLORRHAPHOUS DIPTERA.

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A study of the terminal abdominal segments of male Cyclorrhapha has indicated that the generally accepted views concerning the interpretation of the segments of the postabdomen of these Diptera need revising. A detailed discussion of the terminalia of male Cyclorrhapha in general will be published elsewhere, but the main points brought out by this study may be briefly indicated here.

The normal relation of the sternites to the tergites in the postabdomen of one of the Nematocera in which there is no torsion of the terminal abdominal segments, is illustrated by the bibionid *Dilophus* shown in Fig. 1. The spiracles of the eighth abdominal segment are atrophied in this bibionid, the last pair of abdominal spiracles being those of the seventh segment—as is typical of male Diptera in general. The eighth abdominal sternite *8s* is considerably enlarged in the bibionid shown in Fig. 1, and this condition persists in the higher Diptera, since the inverted eighth abdominal sternite is usually the largest pregenital sternite of the postabdomen of male Cyclorrhapha.

The Orthorrhapha Brachycera occupy a position intermediate between the Nematocera and the Cyclorrhapha, and some of them, such as the dolichopodid *Argyra* shown in Fig. 2, illustrate a stage in the development of the cyclorrhaphous type of male terminalia. Thus in the dolichopodid shown in Fig. 2, the ninth segment *9t* has undergone a complete circumversion, and the eighth sternite *8s* has become drawn up into the insect's left side, although the eighth sternite is not completely inverted in the dolichopodid shown in Fig. 2, as it is in typical male Cyclorrhapha. The seventh sternite

is not "lateroverted" (or displaced into the insect's left side) in the dolichopodid shown in Fig. 2, as it is in male Cyclorrhapha, but the fifth abdominal sternite *5s* is "cleft" posteriorly in this dolichopodid, as it is in many muscoid flies.

The Syrphidae occupy a position at the base of the lines of descent of the Cyclorrhapha in general, and some Syrphidae, such as *Sericomyia chrysotoxoides,* illustrate the beginnings of the modifications characteristic of the higher Cyclorrhapha, since the ninth abdominal segment of *Sericomyia* is twisted about, and the eighth sternite is almost completely inverted, while the seventh sternite is slightly displaced into the insect's left side, but the seventh sternite is not united with the inverted eighth sternite in *Sericomyia.*

In a higher syrphid such as *Paragus tibialis,* the seventh sternite becomes more pronouncedly displaced into the insect's left side than it is in the lower syrphids, but the seventh sternite is still distinct from the inverted eighth sternite in *Paragus tibialis.* In the other species of *Paragus,* however, (as in the case in *Paragus bicolor,* shown in Fig. 3) the lateroverted seventh sternite *7s* unites with the inverted eighth sternite *8s,* and the two sternites are separated only by a faint incomplete suture.

The sixth sternite *6s* is asymmetrically developed in the higher syrphid shown in Fig. 3, being well developed only in the insect's left side—as is also the case in the higher Cyclorrhapha next to be considered. The fifth sternite *5s* is narrowed mesally in this syrphid, and is developed only laterally (on each side) thus suggesting the beginning of the formation of the bilobed fifth sternite typical of male muscoid flies.

The higher Syrphidae thus presage, so to speak, the modifications of the terminal abdominal segments characteristic of the higher Cyclorrhapha, and such features as the asymmetrically developed sixth sternite *6s,* the united lateroverted seventh sternite *7s* and inverted eighth sternite *8s,* etc., of the higher syrphid in Fig. 3, are strikingly suggestive of the modifications of the corresponding sternites in the higher Cyclorrhapha shown in Figs. 4 and 6.

In the helomyzid *Neoleria crassipes* shown in Fig. 4, the relation of the parts of the postabdomen to each other clearly indicates a modification in the direction of the development of the parts characteristic of typical male muscoid Diptera, but the parts remain in a more primitive condition in this helomyzid than is the case in typical muscoid flies, and it is an easy matter to compare the sixth, seventh and eighth sternites (bearing the labels *6s, 7s* and *8s* in

Fig. 4) of *Neoleria,* with the corresponding sternites in such a syrphid as the one shown in Fig. 3.

In the helomyzid shown in Fig. 4, the ninth segment *9t* (together with the proctiger, or anus-bearing terminal region) has undergone a complete circumversion in a clockwise direction (as the insect is viewed from behind), as is typical of the Cyclorrhapha in general, in which the circumversion of the parts is indicated by a looping up of the vas deferens, or ejaculatory duct, over the top of the hindgut before it discharges through the ventrally located intromittent organ of the male. The rotated ninth segment projects more directly backward in *Neoleria* (and in the higher Cyclorrhapha in general) than it does in the syrphid shown in Fig. 3, in which the ninth segment is twisted about, and projects laterally, instead of projecting more rigidly backward.

The eighth sternite *8s* is completely inverted in the helomyzid shown in Fig. 4, as in the case in the higher Cyclorrhapha in general. The seventh sternite *7s* is lateroverted, or is drawn up into the insect's left side, in *Neoleria,* but the seventh sternite is merely attached by one corner to the inverted eighth sternite, instead of being broadly joined to the latter, in this helomyzid.

The sixth sternite *6s* is asymmetrical (being well developed only in the insect's left side) in the helomyzid shown in Fig. 4, and the sixth sternite has become attached by one corner to the lateroverted seventh sternite *7s,* as the asymmetrical sixth sternite tends to do in the muscoid flies and their relatives. The sixth sternite *6s,* however, retains its normal relation to the reduced sixth tergite *6t* in *Neoleria,* and it is an easy matter to compare the sixth, seventh and eighth sternites of the helomyzid shown in Fig. 4, with the corresponding parts in a more primitive cyclorrhaphan, such as the syrphid shown in Fig. 3, or with a more specialized cyclorrhaphan, such as the anthomyiid shown in Fig. 6.

In the anthomyiid *Hylemyia antiqua* shown in Fig. 6, the parts of the postabdomen have become more closely united than is the case in the helomyzid shown in Fig. 4, but it is very easy to compare the asymmetrical sixth sternite *6s,* the lateroverted seventh sternite *7s,* the inverted eighth sternite *8s,* and the reduced sixth tergite *6t,* of the anthomyiid shown in Fig. 6, with the corresponding parts of the helomyzid shown in Fig. 4.

The ninth segment *9t* (together with the proctiger) has undergone a complete circumversion in *Hylemyia,* as is indicated by a looping up of the vas deferens, etc., over the top of the hindgut, and the same is true of the Cyclorrhapha in general.

The lateroverted seventh sternite, *7s,* has united with the inverted eighth sternite, *8s,* in the anthomyiid shown in Fig. 6, but the two sternites are separated by an incomplete suture in this insect. The size of the demarked area of the seventh sternite in Fig. 6, indicates that the seventh sternite undergoes considerable reduction in uniting with the inverted eighth sternite in the anthomyiids and in the muscoid Diptera in general. The area labelled *7s* in Fig. 6 bears the left spiracle of the seventh abdominal segment, and since the spiracles are typically located in the tergites in the muscoid flies, it is evident that a small upper portion of the region labelled *7s* in Fig. 6 is formed by the vestigial tergite of the seventh abdominal segment.

The sixth sternite *6s* is asymmetrically developed in the anthomyiid shown in Fig. 6, and the sixth sternite forms a slender transverse band bordering the genital pouch (into which the aedeagus is thrust in repose) in this insect, as is also the case in the muscoid flies in general. The sixth sternite is attached by one corner to the area representing the lateroverted seventh sternite *7s* in the anthomyiid shown in Fig. 6 (as is characteristic of the muscoid flies in general), and the sixth sternite is frequently mistaken for the eighth sternite in the higher Cyclorrhapha, although the sixth sternite *6s* is situated below the reduced sixth tergite *6t* in Fig. 6, and the spiracle of the sixth abdominal segment lies in the membrane between the sixth tergite and the narrow sclerite in question, as would be expected if this sclerite represents the sixth sternite in these insects.

The fifth sternite *5s* is bilobed in *Hylemyia,* as it is in typical muscoid flies (although the fifth sternite is not bilobed in the helomyzid shown in Fig. 4), and the fifth tergite *5t* is well developed and forms the last tergite of the preabdomen in *Hylemyia,* as is typical of the Muscoidea in general.

The modifications of the sixth, seventh and eighth sternites, bearing the labels *6s, 7s* and *8s* in the anthomyiid shown in Fig. 6, represent a condition intermediate between that exhibited by the corresponding parts in the helomyzid shown in Fig. 4, and those of the calliphorid fly shown in Fig. 5, which has been selected to illustrate the parts of the male terminalia in a typical muscoid fly.

In the calliphorid *Phormia regina* shown in Fig. 5, and in the Muscoidea in general, the ninth segment *9t* (together with the proctiger, or anus-bearing terminal region) has undergone a complete circumversion, as is indicated by a looping up of the vas deferens over the top of the hindgut.

In the Sarcophagidae and related flies, the ninth segment is usually referred to as the "second genital segment," while the segmental complex bearing the label *7s* + *8s* in Fig. 5, is usually called the "first genital segment" by the students of the Sarcophagidae and related flies. The so-called first genital "segment," however, is a segmental complex largely composed of the lateroverted seventh sternite and the inverted eighth sternite, as may be seen by comparing the region bearing the label *7s* + *8s* in Fig. 5, with the parts bearing the labels *7s* and *8s* in Figs. 6, 4 and 3; and the position of the spiracles will also aid in comparing the parts in these flies.

The sclerite bearing the label *7s* + *8s* in Fig. 5 is regarded as a "tergite" by everyone who has attempted to identify it in the muscoid flies, and even in Snodgrass' recent "Principles of Insect Morphology" it is referred to as the eighth tergite in these flies, while the sixth sternite, labelled *6s* in Fig. 5, is regarded as the true eighth sternite by Snodgrass. If, however, the crevice between the lateroverted seventh sternite *7s* and the inverted eighth sternite *8s* of Fig. 4 were to become closed, a condition like that shown in Fig. 6 would result, and if the suture between the lateroverted seventh sternite *7s* and the inverted eighth sternite *8s* in Fig. 6 were to drop out, a condition like that shown in Fig. 5 would result, so that by tracing the parts from Fig. 5 to Fig. 6, and on back through Fig. 4 to Fig. 3, etc., it is readily seen that the structure regarded as a pregenital "tergite" in such a muscoid fly as the one shown in Fig. 5, is in reality a composite region composed of the seventh and eighth sternites, which become drawn up into the dorsal region when the ninth segment undergoes a circumversion.

The validity of the claim that the seventh sternite becomes drawn up into the insect's left side, and that the eighth sternite becomes inverted when a circumversion of the ninth segment takes place, rests wholly upon the assumption that the torsion of the parts of the postabdomen has taken place in a clockwise direction (i.e., from left to right, as the insect is viewed from behind), since a torsion in the opposite direction would produce a wholly different arrangement of the parts from that described above. There is abundant proof that the torsion has taken place in a clockwise direction in the Cyclorrhapha, however, since the looping-up of the vas deferens over the top of the hindgut always takes place from left to right, indicating that the torsion of the parts has been from left to right in every case. Schraeder, 1927, has observed such a

circumversion of the terminalia in the pupal stage of the typical muscoid fly *Calliphora,* in which the arrangement of the parts is exactly like that occurring in the rest of the Muscoidea and their relatives, and the natural inference is that such a circumversion of the terminalia takes place in the pupal stages of the Cyclorrhapha in general. Furthermore, it is easy to trace the clockwise torsion of the parts in a series of Syrphidae, and since the sternites of such a syrphid as the one shown in Fig. 3 are clearly homologous with the sternites bearing the same labels in the series of flies shown in Figs. 4, 6 and 5, it is evident that the interpretation of the parts proposed above is fully supported by all of the available evidence.

The fact that the sixth sternite *6s* of the calliphorid fly shown in Fig. 5 is attached by one corner to the supposed eighth "tergite," bearing the label *7s* + *8s* in Fig. 5, has caused some investigators to interpret it as the "eighth" sternite in the muscoid flies. The evidence of comparative anatomy, however, clearly supports the view that the sclerites bearing the labels *6t* and *6s* in the calliphorid shown in Fig. 5 represent the tergite and sternite of the sixth abdominal segment, as may be seen by tracing the parts in the series of flies shown in Figs. 5, 6, 4 and 3, which lead back to the lower syrphid types in which the tergite and sternite of the sixth abdominal segment are normally developed. The sixth sternite *6s* is asymmetrical in the calliphorid shown in Fig. 5, being well developed only in the insect's left side, as is also the case with the sixth sternite in the anthomyiid shown in Fig. 6 (compare also Figs. 4 and 3); and the narrow sixth sternite forms a stiffening border for the genital pouch in these flies.

The fifth sternite *5s,* or last sternite of the preabdomen, is bilobed posteriorly in *Phormia,* and this condition is typical of the muscoid flies in general. The fifth tergite *5t* is large in *Phormia,* and forms the last tergite of the preabdomen, as it does in the muscoid flies, in which the fifth tergite is the last "visible" tergite of the abdomen. The fifth pair of spiracles is borne in the fifth tergite and serves to identify it when there is a fusion of the segments in the basal region of the abdomen.

A reduction in the segments of the abdomen takes place in various ways in the Cyclorrhapha. In the muscoid flies the first and second tergites frequently unite, but the composite basal tergite bears two pairs of spiracles in such cases, and the first two sternites usually remain distinct, so that it is usually possible to count the segments in the ventral region, when the basal tergites

unite. The reduction of the segments of the postabdomen is usually brought about by the union of the seventh and eighth segments in the higher Cyclorrhapha, and the sixth tergite may becomes atrophied while the sixth sternite may unite with the seventh in some cases, and in some Cyclorrhapha other segments may drop out, etc.

The anus-bearing, non-segmental telson, and the cercus-bearing eleventh segment, apparently unite with the tenth abdominal segment, to form the proctiger, or anus-bearing segmental complex behind the ninth tergite *9t* of Figs. 5, 6, etc., which is usually referred to as the "tenth" segment alone by the students of the higher Diptera, even when they identify its appendages *ce* with the cerci of lower insects. The cerci, however, are appendages of the eleventh abdominal segment, and if the appendages of the anus-bearing terminal region represent true cerci (and these structures in the Diptera are evidently homologus with the structures generally interpreted as true cerci in the Mecoptera and their relatives) then the cercus-bearing eleventh abdominal segment must also enter into the composition of the terminal anus-bearing structure (or proctiger), and on this account, the latter cannot be interpreted as the tenth abdominal segment alone, as some investigators are inclined to believe.

The surstyli labelled *ss* in the higher Diptera shown in Figs. 3, 4, 5 and 6, are appendages of the ninth tergite *9t,* and should not be homologized with the parts of the male genital forceps labelled *cx* and *st* in a lower dipteron such as the one shown in Fig. 1, as is done by Awati, 1915, Hendel, 1928, Patton, 1932, and other students of the higher Diptera. It is not the surstyli *ss,* but rather the anterior and posterior gonapophyses labelled *a* and *b* in the higher Diptera shown in Figs. 5 and 6, that represent the segments of the genital forceps labelled *cx* and *st* in the lower dipteron shown in Fig. 1, as may be seen by comparing the corresponding parts in one of the lower representatives of the Cyclorrhapha, such as a syrphid, etc., with the parts in a bombyliid, leptid, and other lower forms leading back to the Nematocera.

The genital forceps bearing the labels *cx* and *st* in the lower dipteron shown in Fig. 1, are homologous with the parameres of male Hymenoptera, Coleoptera, etc., and if the structure labelled *a* and *b* in the higher Diptera shown in Figs. 5 and 6 are homologous with the parts labelled *cx* and *st* in Fig. 1, it is quite correct to designate the structures labelled *a* and *b* in Figs. 5 and 6, as the parameres also, as is done by Hendel, 1928, Patton, 1932, and

other students of the higher Diptera, although these investigators apparently do not realize all that is implied in this interpretation, when they proceed to homologize the surstylii *ss* with the genital forceps of the lower Diptera, even when they interpret the anterior and posterior gonapophyses of the higher Diptera as parameres!

A more detailed comparison of the gonapophyses, etc., of the lower Cyclorrhapha, such as the Syrphidae, *etc.,* with the parts of the genital forceps of the Bombyliidae, Asilidae, Dolichopodidae, Empidae, Leptidae, and other forms leading back to the Nematocera, will be discussed in a later paper, since it is the purpose of the present discussion merely to present very briefly, the evidence for a new interpretation of the segmentation of the postabdomen of the higher Diptera, suggested by a recent study of the terminalia of male cyclorrhaphous Diptera.

Abbreviations Used in Plate.

a—Anterior gonapophysis (compare with *cx* of Fig. 1). *ae*—Aedeagus or phallosome. *b*—Posterior gonapophysis (compare with *st* of Fig. 1). *c*—Genital spine. *ce*—Cercus. *cx*—So-called "coxite" or basal segment of parameres. *s*—Sternite. *ss*—Surstyli. *st*—So-called "stylus" or distal segment of parameres. *t*—Tergite.

Explanation of Plate VII.

Fig. 1.—A bibionid *Dilophus* sp. Fig. 2.—A dolichopodid *Argyra* sp. Fig. 3.—A syrphid *Paragus bicolor.* Fig. 4.—A helomyzid *Neoleria crassipes.* Fig. 5.—A calliphorid *Phormia regina.* Fig. 6.—An anthomyiid *Hylemyia antiqua.* All figures represent lateral views of the terminal abdominal structures of male insects.